THE NEW FLORA OF KRAKATAU

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IN August, 1883, there occurred in the Straits of Sunda, between Java and Sumatra, the most violent volcanic eruption of which there is any record. This catastrophe involved the island of Krakatau (Krakatoa, as it is usually written in English), as well as the two small neighboring islands, Verlaten and Lang Island. As a result of this eruption about two thirds of the larger island, which was nine kilometers long and five in width, disappeared, while the other islands were noticeably increased in size, and the whole floor of the ocean in the vicinity was completely changed. It was estimated that the total amount of matter ejected during the successive eruptions from May to August amounted to eighteen cubic kilometers, and this immense mass of stones, ashes and volcanic dust was scattered over an enormous area, the ashes being carried many hundred miles, and life of all kinds upon the islands was completely annihilated. Many will recall the brilliant crimson sunset skies that were observed all over the world some months later. These were caused by the presence of fine volcanic dust from Krakatau which, suspended in the upper atmosphere, was carried entirely around the world. The detonations from the explosions were said to have been heard nearly three thousand miles away; and at Buiten-

zorg and Batavia, in Java, about 150 kilometers away, the explosions were likened to the discharge of cannon near at hand, and were so violent as to shake the houses to such an extent that objects were thrown down.

The effect of the great mass of hot ashes and pumice that completely covered the islands, was to entirely destroy every vestige of the luxuriant vegetation which before the eruption clothed the island of Krakatau with a dense forest extending from the shore to the summit of the highest peak, *Rakata,* 832 meters in height.

The island of Krakatau, therefore, after the eruption, was very efficiently sterilized, and offered a most unusual opportunity for studying the establishment of the vegetation upon a large area absolutely barren and comparatively isolated. The nearest land is an island some nineteen kilometers distant on which the vegetation was also largely destroyed, while the large islands of Java and Sumatra are respectively 35 and 45 kilometers distant.

Fortunately there was a man who fully appreciated the importance of this unique opportunity, and determined to trace the reestablishment of the new flora upon the desolated island. The botanical world owes a great debt to Professor Treub, the distinguished botanist who has done so much to advance the study of botany in the tropics, both by his own important investigations and by the building up of the unrivaled facilities for research offered by the magnificent gardens and experiment stations in Java.

Treub's visit was made in 1886, three years after the eruption, and subsequently the island was again visited by him in 1897, and a third expedition was made in 1905.

In the spring of 1906, while engaged in botanical study at the mountain station Tjibodas, in Java, I received word that a visit to Krakatau was being arranged for, and was invited to join it. The results of this trip have been presented in admirable fashion by Professor A.

Ernst,[1] of the University of Zürich, to whose efforts and energy the successful results of this trip were largely due. Considering the very brief time at our disposal, the amount of material secured by Professor Ernst and the completeness with which it was worked out were really remarkable.

On the morning of April 24 our little party set sail from Tandjong Priok, the harbor of Batavia, for our brief cruise among the islands of the Straits of Sunda, for Krakatau. The little coasting steamer "Snip" (Snipe), which had been placed at our disposal for the trip, proved most comfortable, and her captain did everything possible to make our trip a pleasant one. The party included, besides Professor Ernst, Mr. C. A. Backer, of the Buitenzorg Gardens, whose intimate acquaintance with the Malaysian flora was very much appreciated, and Dr. A. A. Pulle, of the University of Utrecht, who, like myself, was working at Buitenzorg. The weather proved all that could be asked, and the voyage over the calm, dazzling blue sea among the picturesque islands was one long to be remembered. As we sailed out of the harbor we could see in the distance the great volcanoes Salak and Gedeh, which dominate Buitenzorg, and which had become quite like old friends. On the slopes of Gedeh lies the mountain station Tjibodas, where I had spent several happy weeks, and to which I was going back on my return from Krakatau. Opportunity was given us to stop at several points *en route,* one being Vlakke Hoek, the southernmost point of the westerly peninsula of Sumatra. All of the places where we stopped showed a most interesting strand flora, including many striking plants, some of which we encountered again on the shores of Krakatau. The shallow lagoons within the coral reefs of these islands were full of interesting things, corals, sea anemones, gorgeously

[1] The New Flora of the Volcanic Island of Krakatau.'' By A. Ernst, Ph.D., professor of botany in the University of Zürich. Translated by A. C. Seward, F.R.S., professor of botany in the University of Cambridge. Cambridge, at the University Press, 1908.

colored fish and many interesting algæ. Professor Ernst collected a large number of striking siphoneous algæ which abound among the coral reefs. (For a list of the plants collected at these intermediate stations, see Professor Ernst's Memoir, pages 9 to 18.)

Vlakke Hoek was devastated by the great waves resulting from the eruption of Krakatau, the waves reaching a depth of fifteen meters and sweeping away practically everything except the great iron light house tower, which alone remains of buildings existing before the eruption.

From Vlakke Hoek we crossed the Straits of Sunda to the southwest coast of Java (Java's first point), and *en route* had our first view of the peak of Krakatau rising above the clouds to the east. The bold shores of the Javanese coast presented a great contrast to the flat, monotonous shore at Vlakke Hoek in Sumatra. The difference in the topography of the land is reflected in the plants, which were strikingly different from those of Vlakke Hoek (see Ernst, pages 24 to 26). Early in the morning of April 26, we approached the Krakatau group of islands.

The view of the island of Krakatau from the north is most impressive. During the great eruption the volcanic peak Rakata was cleft down the middle, so that from peak to base its northern side presents a perpendicular cliff half a mile high, falling sheer into the sea, which at the foot of the cliff is now more than three hundred meters deep. The exposed face of the cliff forms a perfect median section of the cone, and the arrangement of the rocks of which it is built up offers a most extraordinary picture. Professor Ernst took some admirable photographs, which are reproduced in Plate III of his Memoir.

At six o'clock we dropped anchor and soon after were taken ashore in one of the ship's boats. The landing was made on the east side of the island where the outer part of the beach forms a broad zone of mingled pumice, coral and all sorts of débris; fragments of driftwood, seaweed

and a conglomeration of seeds and fruits washed up by the tide.   Many of the fruits washed upon the shore were those of characteristic strand plants like cocoanuts, screw pines, Nipa palms and others.   Most of these show various devices for facilitating their transport by water, and some of them had germinated and were trying to get a foothold in the loose mass of pumice and coral sand.

Above this outer drift zone there is a characteristic sandy belt where various typical strand plants have established themselves.   The long prostrate stems of *Ipomœa pes-capræ*, that most ubiquitous of tropical strand plants, sprawled over the sand, and with these were masses of the curious grass, Spinifex, and a yellow flowered leguminous plant *Vigna lutea*, a euphorbia with thick, waxy leaves, and various other species common to the outer littoral zone of the Indo-malaysian region. While fruits of the Nipa palm were found, the plant has not yet got a foothold in Krakatau, and there is as yet no mangrove formation established.

Back of the beach a thrifty belt of forest is conspicuous and could be plainly seen long before we reached the island.   Some of the trees in this forest are at least fifty feet high, the tallest being specimens of the curious *Casuarina equisetifolia* Forst., a genus mainly confined to the Australasian region, but with a few species widely distributed throughout the Malayan Archipelago.   Associated with these were found specimens of screw pines (Pandanus sp.), and the striking *Terminalia Catappa* L., whose whorled branches and great shining leaves make it one of the most notable of tropical trees.   Perhaps the most beautiful of all the trees of this strand forest is *Barringtonia speciosa* Forst., a tree with large, glossy, dark green leaves and great white flowers with a crown of stamens looking like an enormous myrtle flower.   The curious four-sided angular fruits of this tree are very common along the beach.   Of the few climbing plants the most conspicuous was *Vitis trifolia* L.

After spending some time exploring the beach and

strand forest, we pushed inland toward the south, not without much exertion and perspiration. The unclouded rays of an equatorial sun beat down pitilessly upon us, and when, after struggling over blocks of pumice and through thickets of tall grasses and bushes, we finally reached a small grove of cocoanut palms, full of fruit, we threw ourselves down on the ground under their grateful shade and took a well-earned rest. No time was lost in sending one of the natives up into a tree for green nuts, which were thrown down and quickly opened, and never did anything taste better than the cool, sparkling cocoanut water after our exhausting march through the fierce heat of the jungle.

From the ship we had seen that the ravines on the flank of the Rakata were filled with a dense growth of trees, forming the beginning of a new forest, but it was quite impossible to guess what the trees were. We tried to cross the open tract lying between the belt of forest on the shore and the cone in the center of the island, but we had to give up the attempt after penetrating some distance inland, following the dry bed of a stream for part of the way. The land was terribly rough and covered in many places with a dense jungle of grasses ten or fifteen feet high, through which he had to hew a path with the wicked-looking cutlasses which every Malay carries when traveling. The way lay over steep ridges, which grew worse and worse as we approached the cone, and finally we realized that with the short time at our disposal, and the limited means of cutting our way through the jungle and scrub, we should have to give up the attempt, which we did very reluctantly, and retraced our steps to the shore, where we embarked for the ship.

The monotony of the journey over the grass steppes in the interior of the island was broken by encounters with countless ants which built their nests everywhere, in the crevices of the rocks, among the roots of the grasses and shrubs, and even hanging from the branches of the shrubs and trees; and as we scrambled up the steep slopes

of the frequent small ravines, down would come showers of ants, swarming all over us but not doing any serious damage. Few showy flowers were seen, the most striking being several terrestrial orchids, one of which *Arundina speciosa* Bl. was quite common and decidedly handsome.

After boarding the ship, we sat sail for the north side of the island, where a landing was made at the base of the rock wall formed by the fractured face of the riven cone of Rakata. As we approached the face of the cliff, we were startled to see what looked like puffs of smoke rising from various fissures in the cliff. Remembering the history of the mountain, and also having just received the news of the eruption of Vesuvius and the terrible earthquake at home, the thought occurred that perhaps Krakatau was getting ready for another outburst, which to say the least, was not reassuring. But we finally discovered that the "smoke" was merely clouds of dust caused by the falling of débris from the face of the cliff.

Our landing was made in a broad bay where there is a narrow beach, but the development of the strand flora is much less advanced than on the south side of the island. Ferns were noticeably abundant, as they were on the other parts of the island when it was first visited after the eruption. *Nephrolepis exaltata* Schott was especially frequent, and in the crevices in the rocks we found numerous prothallia and young plants of a species of Gymnogramme and of several other ferns. Some of the ferns and other plants which were growing upon the ground here are usually epiphytes. Of these *Polypodium quercifolium* L. was the most conspicuous.

After exploring the interior and strip of land at the base of the cone, we returned to the ship. Before the sun went down we set sail for Java and soon the peak of Krakatau was left behind us. The next morning found us safely back in Tandjong Priok.

The Reestablishment of the Flora on Krakatau

When the island was first visited by a geological expedition two months after the eruption, the whole surface was buried under a layer of ashes and pumice averaging thirty meters in depth, and in some places as much as sixty meters.   Thus, of course, every trace of life must have been quite annihilated and the sterilization was complete.   An analysis of the ashes showed that, except for phosphorus and nitrogen, all of the elements necessary for plant life were present.   (See Ernst, p. 50.)   Ernst suggests that the other elements necessary for the establishment of a new flora were conveyed from the mainland in the form of dust, and that as a result of the intense electrical activity which accompanies the almost daily rains of the equatorial region, the atmospheric nitrogen is oxidized into the nitric and nitrous acids which furnish the necessary nitrogen.   This with the salts and traces of organic matter in the ashes would have been sufficient in a very short time to allow the establishment of the first micro-organisms upon the island.

The first botanical expedition, as already stated, was made under the direction of Professor Treub in 1886, three years after the eruption.   During this interval a considerable number of plants had already established themselves upon the island.   The most important fact brought out by this trip was the great importance of the blue-green algæ in the early establishment of the new vegetation.   Thin blackish, slimy films, formed by a number of species of Oscillatoria and other blue-green forms, were found in great quantity coating the surface of the ashes, and the gelatinous matrix of these low plants offered a substratum which was favorable for the germination of the spores of ferns and even for the seeds of a few phanerogams.   It was found that the colonization of the island was quite as marked in the interior and upon the high cone as it was along the shore, but the plants of the interior of the island were for the most part

quite different.   A remarkable fact was the great pre-
ponderance of ferns in the new flora.   In the period of
three years no less than eleven species had established
themselves and formed the predominant feature of the
new vegetation.   In our visit to the north side of the
island, where the reestablishment of the vegetation, as
we have seen, was less advanced than on the south side,
this preponderance of ferns was very marked, whereas
in the other parts of the island they have been to a very
great part supplanted by the phænogamous immigrants
and several species seem to have disappeared.   In the
drift zone of the beach Treub found nine species of
seedling plants, and in the central part of the island
eight, two of which were the same as those upon the shore.
Of the remaining six, four were composites and two
grasses, all forms which would be distributed readily
by the wind.   These phanerogams, however, were far
less numerous as individuals than were the ferns.

A series of visits to the islands was projected by Treub,
but unfortunately the plan could not be carried out, and it
was not until 1897 that a second expedition visited Kra-
katau.   This second expedition was also under Treub's
direction.   In the interval of more than ten years that
had elapsed since the first visit the number of plants had
greatly increased and most of the island was covered
with vegetation which began to show the characteristic
formations which are now so conspicuous.   The *"Pes-
capræ"* formation, *i. e.,* the beach zone characterized by
the predominance of *Ipomœa pes-capræ,* was well estab-
lished, but the belt of strand forest now so marked upon
the southern side of the island was entirely wanting in
Krakatau, but the beginning of such a forest was found
upon the neighboring Verlaten Island.   Almost no trees
were met with, and even shrubby plants were not numer-
ous.   The grassy "steppe" lying between the beach and
the base of the cone was conspicuous and probably not
very different from its present condition.   The total
number of vascular plants collected on this second ex-

pedition amounted to sixty-two, of which twelve were pteridophytes and fifty phanerogams. The ferns still predominated in number of individuals.

A third party visited the island in 1905, but the results of this expedition have not yet been published.

A very full account of the present flora is given by Ernst (pp. 37 to 48). In the three expeditions the results of which have been published a total of 137 species is recorded. While a very large majority of these are phanerogams, representatives of all the principal groups of plants have been collected. In the earlier expeditions the preponderance of ferns, as we have seen, was very noticeable, but at present this is not the case and they have largely given place to the more aggressive phanerogams. We collected only six species of ferns and one of Lycopodium, the wide spread *L. cernuum,* while on the first and second expeditions eleven species were noted, and although it is true that we failed to reach the center of the island, where in all probability other species would have been encountered, it may be noted that we collected seventy-three species of phanerogams against forty-eight species recorded at the time of the second expedition.

Of the lower plants only two species of mosses have been collected and a single species of antheroceros (this was found only on the second expedition). We found the two species of mosses growing fairly abundantly, but no liverworts. Whether the latter grow in the central part of the island remains to be seen, but it is highly probable that some of the very numerous species of Java and Sumatra will be found there. The scarcity of bryophytes is remarkable, as it is generally assumed that their spores are readily disseminated; and the contrast with the ferns which so quickly colonized the island is most striking. Three species of fleshy fungi have been collected and a considerable number of species of diatoms and blue-green algæ were among the earliest settlers of the island.

Professor Ernst made some interesting studies on the

bacteria, collecting from several places samples of soil which were placed in sterilized tubes. These were examined by Dr. E. De Kruyff, bacteriologist of the Agricultural Department at Buitenzorg, and the soil was found to contain the usual proportion of bacterial forms, both ordinary soil bacteria and putrefactive types. An interesting discovery was the presence of a new aerobic nitrogen-fixing bacterium, which was named *Bacterium krakataui. B. radicicola* is present in abundance in the root tubercles of the numerous leguminous plants which now abound on the island. It is evident that the different kinds of bacteria must have very early established a foothold upon the sterilized island surface and were no doubt among the factors which rendered the establishment of the higher types of vegetation possible.

A most interesting find was a single thrifty female specimen of *Cycas circinalis*. This tree had a trunk nearly two meters in height, and the size of the plant suggested that it was a survivor of the original flora; but Ernst states that this is impossible, as the portion of the island where it is growing belongs to the new shore formed since the eruption.

AGENTS IN DISTRIBUTION

Ernst has treated very fully the question of the agents by which most of the members of the new flora were introduced (pages 53 to 68). There seems no doubt that the earliest immigrants—bacteria, blue-green algæ, ferns and mosses, were wind borne, and the same is probably true of the first phanerogams found upon the island, composites and grasses, but other agents have been active in transporting seeds and fruits to the shore of the devastated island, and of these the ocean currents have probably been most important. There is no question that the fruits and seeds of the strand plants are probably all water borne, and Ernst called attention to the important part played by driftwood in introducing new plants whose seeds might have been lodged in the crevices in the

bark, or he even suggests the possibility of young plants being transported on uprooted trees. The shore of the island is covered with masses of logs and fragments of trees which might very well have brought with them not only vegetable immigrants, but animals as well. An interesting case was that of the two species of fleshy fungi, Polystictus, which were found growing upon logs lying on the shore, and whose mycelium almost certainly had been growing in the logs before they were drifted out to sea.

Birds have undoubtedly also played their part in the introduction of seeds, especially those of fleshy fruits such as the species of Vitis, common near the shore, and several species of figs found somewhat further inland.

The rapid development of the vegetation in the nine years between the visit to the island in 1897 and our visit in 1906, and especially the great increase in the forest vegetation, makes it evident that before very long the forest which originally covered the island will be again in possession. Already the belt of forest along the shore is working inland, and it is to be expected that the patches of forest in the ravines flanking the cone in the interior of the island are spreading shoreward, so that in the course of time the intermediate belt of grassy land will probably be completely obliterated and the forest will once more be in undisputed possession of the entire island.

A MALE CRAYFISH WITH SOME FEMALE ORGANS

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The crayfish to be described here was peculiar in being a male with some few of the external characters of a female. If by the term gynandromorph we understand an individual that shows both male and female organs in different parts of the body, though the normal individuals have but one set of sexual characters, we may call this crayfish a gynandromorph.

Compared with other known cases of mingled sex in the crayfishes this one is peculiar in being chiefly all male, while most of the other cases on record are predominantly female.

Before describing this crayfish it will be useful to recall that the sexual organs of crayfishes consist of the gonads, ovary and testis, their ducts, certain modified limbs to ensure the transfer of the sperm to the female from the male; and in the crayfishes of the genus Cambarus, a sperm receptacle upon the female in which to store up the sperm till the time the eggs are laid.

The ovary of the female is a median mass that becomes filled by the large eggs and from it an oviduct passes down on each side of the body to open out upon the base of the antepenultimate leg, right and left, as a rounded hole that is closed by an operculum, except at the time of egg laying.

The testis of the male is a similar but smaller body from which a convoluted duct leads down each side to open out on the base of the ultimate leg at the tip of a perceptible papilla which is turgid with the pressure of the blood.

The limbs of the female are reduced, or absent, upon the

first somite of the abdomen, while those on the second are like the following ones.   But the limbs on the first somite of the abdomen of the male are quite remarkable conduits that conduct the sperm; and the limbs of the second somite are peculiarly adapted to fit against the first as a necessary part of this sperm-transferring apparatus. The limbs of the thorax may also be modified so that some of them bear hooks for holding the female.

In the case of Cambarus the female sperm-receptacle is a unique median pocket in the shell, which is of as much physiological necessity for the race as are the ovary, the testis and the male appendages that transfer the sperm.

The gynandromorphic crayfish to be described was a small sized and probably immature male of the species *Cambarus affinis*, taken in a lake at East Hampton, Conn., by Mr. Kenneth N. Atkins.[1]

The external appearance of this specimen was that of a male 55 mm. long with small chelæ only 30 mm. long, having the hand 15 mm. long and 5 mm. deep.   The antennæ were 45 mm. long.   The papillæ of the fifth or ultimate legs seemed normal. The second abdominal limbs were as usual in a male but the first were of the puerile or so-called second form of male limb very like that found in a young normal male five months old and 38 mm. long.   The tips were blunt and there was a free joint above the basal joint.   The attaching hooks of the third, or antepenultimate, legs were short and blunt, but normal for the young male.   There were the usual long male hairs on the spine between the ultimate legs, and

[1] The finding of this species in this locality is of interest as bearing upon the geographical distribution of crayfishes. New England being singular in the fewness of its crayfishes, which are largely restricted to the drainage into the St. Lawrence, the question to be settled is whether the crayfishes are absent because they never got there or because some characteristics of climate, soil or biological environment are inimical to them. It seems that these crayfishes were first observed in this lake some nine years ago, being, it is thought, brought there by fishermen. Since these crayfish are fairly abundant there now this is evidence that crayfish can live in this region, and favorable to the idea that the relative absence of crayfishes throughout these states is due to their not having migrated in there.

no sign of any female organ, the sperm receptacle, anterior to it.

To these male external features there were added the two female openings on the antepenultimate legs.   On the right the basal segment of the leg bore a well-formed normal female orifice, that is, a soft, round, depressable area, or operculum.   This opened along the median edge as a curved mouth bounded by a narrow stiff rim of hard shell.   On the left the opercular area was perhaps somewhat less perfect, its median side being more a straight line which opened as a mouth, and the curved bounds were more vague.   The hard rim was thicker, apparently by the amount that the straight mouth should have been curved to make the normal contour.

On dissection the internal organs were found to be entirely those of a male, for the above female openings had no connection with the interior and there were no oviducts nor ovaries.   On the right the operculum, when pushed in, showed a short conical pocket that received a needle point but appeared to end blindly as a mere thin chitinous continuation of the shell inwards.   This pocket was flat.   The mouth was a little more than 1 mm. long and the pocket slightly shorter than the mouth, on the right side.   On the left the mouth slit led into a pocket of less extent.

The essential internal organs of this animal were the testis and the two efferent ducts.   The testis was a median mass some 3 mm. long under the heart, with two anterior lobes about 2 mm. long rising upwards in front of the heart.   Besides this well-developed part the testis was continued back over the intestine as a short minute membranous thread and forward between the stomach and the hepato-pancreas as a clear tubular membrane, or sterile part of the testis about 2 mm long, from the right and from the left lobe.

Where the right and left lobes joined the median lobe the different duct sprang out each side and, passing back alongside of the median lobe some 3 mm., went away at

right angles over the surface of the dorsal muscle-mass
that comes into the thorax from the abdomen on the
side of the thorax, without any coils or turns, some 4
mm. Each duct then descended in a slightly sinuous
course to the projecting base to which the antepenultimate
leg is attached, where it became thicker and, making a
short semicircular curve, entered the basal joint of the
leg and passed straight out to the tip of the papilla.
The duct contained sperm.

Comparing these findings with the anatomy of normal
young males and females of the same species, we see that
in a male of 65 mm. killed in October the first pair of
limbs on the abdomen have much more perfected tips
and lack the joint near the base; while internally the
sperm ducts that lie alongside of the median part of the
testis are so coiled as to be there about 20 mm. long
instead of 4 mm. The duct was also larger and contained
more sperm. Allowing for the differences in size and
in time of year, the two specimens are essentially alike
and we may regard the abnormal one as perfect in all its
male organs, though they had not reached their final form.
Doubtless this male would have been able to transfer its
sperm to a female in the proper season, that is, in the fall.

Serial sections of the testis show no indications of
any hermaphrodite nature, no ovogenesis in any part.
On the other hand, the different duct and the collecting
tubules contain some nearly mature sperms. Some of
the acini show spermatogonia with equatorial plates.

The two sham oviduct-openings of this specimen when
compared with the real openings of a female of October,
some 60 mm. long, show the closest agreement externally.
But there is the fundamental difference internally that
the normal mouth, instead of leading into a blind, minute
pocket, continues directly as a wide and comparatively
straight tube some 10 mm. upwards to the ovary.

In brief, then, this gynandromorph was a young male
that would have functioned as such at the next breeding
season, yet it presented two female characters, openings

as if to lead to ovaries, but with no internal connections and no discoverable use. These sham openings stand in the proper place for the oviduct openings of a female.

A review of the literature fails to show any abnormal crayfish with just these combinations of male and female characters; in fact, as before stated, most of the known cases are females with some male features. Recorded abnormalities of crayfishes include the cases of repetition of parts in one sex and the cases of mixtures of traits of two sexes. The former have been brought together by Bateson in "Materials for the Study of Variation," Macmillan, 1894, the latter by Hay in "Instances of Hermaphroditism in Crayfishes," Smithsonian Miscellaneous Collections, 1905.

In his monograph on the crayfishes of Pennsylvana Ortmann has recently described five additional cases in Cambarus, in which the external sex organs are more or less mixed and in part defective.

Bateson found that in 586 females of *Astacus fluviatilis* there were 23 abnormal cases. In these, besides the usual openings upon the bases of antepenultimate legs, there were one or two similar openings upon the penultimate, the ultimate or even upon all; making a maximum of three pairs of openings. Moreover, the oviducts generally branched so that more than one pair of oviduct openings might be functional, but in other cases the extra openings might end blindly and be of no use. Of 714 males only one was abnormal and that presented not a duplication, but a suppression of organs, having no trace of a generative opening upon the right side, while the sperm duct of that side hung blindly in the body cavity.

A real case of duplication of sexual characters in a male crayfish was recorded, in a rather inaccessible publication, the *Indiana University Bulletin*, by W. J. Moenkhaus, in 1903. He found in *Cambarus viridis* a male that had in addition to the usual first and second male limbs of the abdomen the third pair modified to exactly resemble the

second, in plan, and to differ from them but slightly in the detail with which this was carried out.

These cases of duplication of external organs must not be confounded with the gynandromorph here described since that has both male openings and female openings and not a mere duplication of the openings of one sex. There is so much difference between the male papillæ of the fifth legs and the operculate openings of the antepenultimate legs of the female that we must regard them as two morphologically and physiologically distinct organs and their occurrence upon the same animal is not the same thing as the duplication of one set upon one animal. This is true even if there were reason to suppose that both kinds of openings may have had some common origin in the past.

The cases of hermaphrodite crayfishes previously on record were considered by Hay along with most interesting new cases. It appears from his paper that there are in crayfishes no known cases of such complete, typical, gynandromorphs as that of the lobster described in 1703 as having both external and internal organs of the male on the left side of the body and of the female on the right. All crayfish gynandromorphs, but one, are really either males or else females as regards the gonads, and have added but some of the external organs of the opposite sex. One is a female with a little testis as well as external organs of the male.

The numerous cases of crayfishes from the southern hemisphere with the external openings of both males and females described by different authors are especially interesting as resembling the gynandromorph of this present paper, since it was found by Lönnberg,[2] that whenever the internal anatomy was made out, the animal had either a testis or an ovary, and if there was a testis the normal ducts led to the normal male openings, while the redundant female openings had no internal connections, though the testis did send out an extra duct towards the

[2] *Zool. Anz.*, 1898.

pseudo-female opening; while if there was an ovary the oviducts went to the normal openings and the extra male openings were of no use, though here again the ovary sent out a duct towards the useless male openings.

The extra openings, however, Lönnberg found to be shams, or closed openings, yet they look like the openings of the opposite sex.

This state of things, the perfect male or female with sham openings and pseudo-ducts of the opposite sex, seems to be the usual, if not the only, condition found in many species of the genus Parastacus, to judge from all the specimens that have been studied. The relationship between Parastacus and Cambarus is, however, believed to be so very remote that one can not suppose the present case of abnormality in a species of Cambarus has any genetic connection with what seems to be the rule in many, but not all, species of Parastacus.

The other recorded gynandromorphs are one specimen of Astacus and fourteen of Cambarus, and all except one are females that have some male characters added. The superfluous male characters are sometimes but the modification of the first abdominal limbs to resemble those of the female, in others both these and the following limbs are just like the male limbs. In one the male attachment hooks, and the male openings and even the hirsute spine posterior to the somite of the sperm receptacle, that is, all the external characters of the male, are present along with normal ovary and oviduct.

This last was the most hermaphroditic of all known crayfishes. It was the female *Cambarus affinis,* 106 mm. long, described by Hay. This seemed externally a male and attempted conjugation with a female, having a good set of male external organs. But internally it had a large ovary with nearly mature eggs and two perfect oviducts. The specimen was thus deficient in lacking the sperm receptacle that a female of this kind of crayfish should have in order to get the eggs fertilized. In addition to the ovary there was a small testis, on the right,

with a duct leading to a single male opening on the ulti-mate leg.   Though no sperm was present it seemed as if sperm might have been made.   It appears that this individual could have been of little or no use to the race.

With this exception all sexually abnormal crayfishes, as far as known, are either males or females with either some duplication of organs that belong to that one sex or else the addition of external organs of the opposite sex.   But in Parastacus there is also some duplication of internal ducts, which needs additional investigation to show how far it is duplication and how far it may be the addition of ducts of the other sex.   As far as Lönnberg's observa-tions go the extra ducts were like the normal of that sex and not like those of the other sex.

The fact that the male may have merely the external openings of the female sex without any internal female organs shows that the gonad is not necessary as a stim-ulus for the making of the external organ, that the ex-ternal organ is not correlated with the gonad by any internal secretion or other means, necessarily.   At the same time Parastacus shows that when there are extra openings, or rather sham openings, the gonad sends extra ducts towards those openings so that there seems a corre-lation between the gonad and the external organ that belongs to the opposite sex.   However, Lönnberg found in some of the testes of Parastacus objects that he thought might be eggs; so that the purity of the gonads is some-what doubtful.

There is a possibility that these males may have had enough development of a hermaphrodite gonad to supply a stimulus to the surface that would make the external female organs begin to develop in the right place for a female having ovaries, though the gonad was essentially male.

The gonads of crayfishes are late in becoming visible in the ontogeny of the individual and the external organs do not show till the eggs have hatched and passed into the third larval stage, after two moults.   Whether these

external organs would develop at all without the internal gonad can only be determined by future experiment, but the abnormal cases above cited show that the external organ may be formed without the gonad of that sex to which the external organ ought to belong and make it probable that the external organs and the gonads are so independent that we need not suppose one leads to the formation of the other.

The sex of the crayfish is not merely the possession of egg or sperm, but of something made evident in a variety of places over the body, as sex organs that are accompanied by the necessary reflexes and instincts to use them.

That the sex is rather intimately dependent upon function seems to be indicated by the occurrence of the two forms of male, known as the first and second, which alternate in such a way that at the breeding season the external organs of the male are perfect, while at another time of year the same male has relapsed into a juvenile state in which the sperm transfer organs are as they were in youth and probably of little or no functional value. These morphological changes are made possible by the shedding of the shell and the growth of what is practically a new organ.

We have then some reason for supposing that back of the visible sex organs there is some state or condition of the organism that can at least modify the structure of the sex organs.

Nothing is known as to the origin of these gynandromorph crayfishes. But regarding the eggs as at first able to make either male or female, or make more than one individual under certain circumstances, the gynandromorph may be looked at as a partial realization of the entire set of possible organs. The causes may lie in physiological states present at various stages of ontogeny. Where a whole species is gynandromorphic the egg may be predestined in the ovary to produce a mixture of organs. When only an occasional individual has

a few external organs added to the normal set the causes may lie in conditions not found till late, after fertilization.

Just as the determination of sex may be due to different conditions in various animals and plants, so the repression or the expression of one or another sex organ may be due to diverse causes acting at various periods of ontogeny, and not to any single factor. Moreover, we do not know how far the gynandromorph may be the result of aberrations independent of the causes of determination of the gonads.

However amongst the insects, where gynandromorphs are well known, there are reasons for restricting our surmises as to the time of origin of the mixed expression of sex organs. Here the mixing seems to be associated with the period of fertilization. In the honey bee the sex is determined, apparently, in fertilization and the phenomenal cases of gynandromorphs, such as those studied by V. Siebold in 1863, in the Eugster hive, have often been explained as due to abnormal fertilizations. This interpretation has been most acutely elaborated by T. H. Morgan on the basis of the facts of experiments upon echinoderms and the results of Toyama upon hybrid moths. He is finally led to the view[3] that the egg nucleus by itself would produce male, the sperm nucleus by itself also male, but the two combined produce female. The gynandromorph would be the result of polyspermy. It would be a sort of combination of individuals, the one female, arising from the part of the egg containing the fused egg and sperm nucleus; the other, male, arising from the part of the egg in which extra sperms developed without contact with the egg nucleus. The female parts of the gynandromorph would have two parents and should be mixed in a hybrid, the male parts would have but one parent and should be pure in a hybrid.

The hypothesis of polyspermic origin of gynandromorphs might be applied to the crayfish with the common assumption of two sorts of sperm, male producing and

[3] This journal, November, 1907.

female producing.[4]   We assume that every egg is fertil-
ized and will be male or female according to the sperm
that unites with its nucleus.   But a gynandromorph
might arise by adding to the male or the female some
organs of the opposite sex due to the independent de-
velopment of the opposite kind of sperm in parts of the
egg.   All sorts of gynandromorphs might be imagined
upon this basis.   Moreover, we might assume the abnor-
mal cases of duplication of sex organs in one individual,
such as studied by Bateson, to be due to the independent
development of sperms that happened to be of the same
kind as the one that fused with the egg nucleus.   In
theory we might even refer the doubleness of organs not
.concerned with sex to some sort of super-fertilization.

Whether such hypotheses have any value may be de-
termined by future experiments in the cross breeding
of crayfish.   Such experiments may enable us to decide
whether gynandromorphs arise before, during or after
fertilization and may throw light upon their causation.
The crayfishes in this part of the world, are especially
well adapted to these experiments, for if crosses can be
obtained at all, we may expect to distinguish between
pure and mixed sex organs, since both the male and the
female have external organs that are at the same time
essential sex organs and characteristic specific characters.

Meanwhile the totality of facts known seems to mean
that the gynandromorph crayfishes are caused by un-
known disturbances, which may happen at various periods
of ontogeny, though probably more often in the ovarian
egg; that these disturbances may have no connection with
the gonads; and that if in some cases the disturbances are
possibly associated with polyspermy, in general they seem
more fundamental and deep seated amidst the causes of
symmetrical form within the egg.

BALTIMORE,
         January 11, 1909.

[4] In some crayfish there are visibly different forms, some are wound
clockwise and some counter clock, some have more and others less rays.

PRESENT PROBLEMS IN PLANT ECOLOGY[1]

IV. PROBLEMS OF LOCAL DISTRIBUTION IN ARID REGIONS

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THE physical conditions prevailing in arid regions are such as render it unsafe to admit without further investigation generalizations regarding their plant life which have been drawn from studies conducted elsewhere. This is sufficient justification of an attempt to analyze certain problems which confront the student of desert ecology in his efforts to apply knowledge or principles drawn from previous experience. These problems have the advantage of a certain clearness of definition, which corresponds in a way with the sharp features of the desert and its characteristic vegetation. Their solution may involve great difficulties, and some of them, with our present methods, may be incapable of solution, but they are, at all events, capable of clear statement.

In the attempt to present such a statement, which may or may not prove successful, I shall for the present limit the discussion to the desert country of the southwestern United States, for the sufficient reason that my own studies have been conducted in that region; and I shall omit all consideration of the higher elevations of the mountains, which, though in the desert, are not of it; so that whatever is said at this time will be understood to apply to the floor of the desert, that is the great plateaus and valleys which from Texas to California lie between the mountain peaks and ranges, together with the long slopes and low hills which border them on every hand and form the natural approach to the mountains.

[1] A series of papers presented before the Botanical Society of America, at the Baltimore meeting, by invitation of the council.

Proceeding in a manner that will be indirectly a record of personal experience, one of the first questions presented to a student of desert botany is this: What are the conditions that determine the successful occupation of a desert habitat by certain plants, but prevent its occupation by others?

It will be necessary at the outset to understand what is meant by a desert habitat, since on this point the popular conception—and possibly that of some botanists—is not clear. There is as much difference between habitats in the desert as in any other region, possibly more, and their definiteness of location and relative sharpness of demarcation form one of the most striking and characteristic features of arid regions. The rivers of the valley trough, such as the Santa Cruz, the Gila and Salt Rivers in Arizona, though inconstant, are none the less the main drainage channels between the adjacent water sheds. Along their banks water-loving willows, cottonwoods and arrow-weed find a congenial home. The adjacent flood plain, with its water table within reach of their roots, is the natural habitat of the mesquite and some other semi-mesophytic species. Within its limits the areas known as salt spots are inhabited by various halophytes, especially by species of *Atriplex* and *Suaeda*. Just beyond the flood plain is the long slope, a most characteristic feature of desert topography, which rises slowly to the foot of the mountains, often miles away, its soil and drainage conditions presenting a sharp contrast to those of the flood plain, and its vegetation being correspondingly different. The low outlying hills, in their turn, present quite as marked peculiarities of soil, and furthermore introduce differences of aspect which are correlated with marked differences of vegetation. In short, the habitats of such a desert region as that of southern Arizona, as far as edaphic relations are concerned, present conditions which vary all the way from distinctly hydrophytic to extreme xerophytic, and all these may be in close proximity.

For all these habitats the fact is to be emphasized that the general climatic conditions are the same, and it is important to note that not a few of the plants which grow where a sufficient or even abundant water supply is assured are nevertheless marked, as a rule, as plants of an arid region by their coriaceous, hairy or otherwise xerophilous leaf structure. The point to be specially noted here is that while plants of the arid, or semi-arid southwest grow in a great variety of habitats, some of which are by no means dry, all are subject to the severe conditions of a desert climate, especially intense insolation, low percentage of atmospheric moisture, and drying winds. The problem, therefore, of the occupation of any one of these habitats is successfully met only by those plants that are already adapted, or are capable of individual adjustment to the dry air and hot sun in which they must live; all others inevitably fail.

This will be made clear by reference to the introduction, or attempted introduction, of various cultivated plants, a subject which presents a most instructive history. The yards of Arizona cities constitute an experiment station in which year by year, at private instead of public expense, the availability of one species after another for desert planting is being determined. From the great number of plants successfully cultivated there seems, at first sight, to be sufficient justification for the reiterated assertion that anything will grow here if you only give it water enough, but closer attention to the actual facts of the case makes it evident that this statement is true only in part, and that there are many plants that will grow only indifferently or not at all under the atmospheric conditions which prevail here, especially in the summer time. To give a few examples, geraniums, the universal easily raised plants of moister regions, are very uncertain, some varieties accommodating themselves fairly well to the desert air, while others fail altogether. Cannas and gladioli, which grow side by side in the east, part company here, the former making a good growth in

Arizona gardens, the latter failing altogether. Those who have handled roses for a period of years have learned what varieties may be expected to do well in the dry air of the desert, and what ones may be counted out, and so on through a long list of plants which, by knowledge gained in the costly school of experience, are coming to be depended on, or are being rejected one after another, as they are found to be unsuited to the environment into which they have been brought. Thus, in a purely empirical way, it has been found that many plants successfully cultivated in regions of greater atmospheric humidity make an entirely normal growth in the desert, if their roots are well supplied with water, but that others, however well cared for in this respect, either fail completely, or come short of making a healthy growth, and that this is especially true in the summer months when desert conditions are most pronounced.

With the accumulation of such facts the more evident does it become that a very complicated problem is here presented. Why is it that one plant, properly watered, does well in the desert, while another, though treated in the same way, makes a poor growth or fails altogether? At first thought it would seem as though there must be a difference in the capacity of the root systems of the two plants for absorption, and that this may be a sufficient explanation of their different behavior; but it is evident on consideration, that with precisely the same capacity for root absorption, a plant in which transpiration is successfully regulated may thrive in an atmosphere in which one subject to excessive transpiration will perish. The most elaborate experiments and the most exact determinations of rate of absorption—assuming that such determinations are possible—would be very likely to throw no light on the problem. Comparisons of the transpiration rate of the plants in question appear more promising, but the same difficulty arises in an attempt to pursue the investigation along this line, for there is no reason to suppose that two plants of widely different rates of trans-

piration can not successfully occupy the same habitat
if their capacity for root absorption differs in the same
ratio.   But supposing that with infinite patience and with
a reasonable approach to accuracy both sets of physio-
logical data have been determined, we are still, quite pos-
sibly, entirely in the dark as to the real cause of the
different behavior of the plants under investigation.   It
may be in their case that the whole matter of absorption,
conduction, and transpiration is beside the mark, and
that certain plants can not succeed in the desert because
the intense insolation exerts directly a prejudicial in-
fluence to which they have not become inured.   The intri-
cate nature of the subject is apparent, and it is also evi-
dent that there is little encouragement for any one to
take it up who has not had extended training and thorough
equipment for physiological research.   Yet with all its
difficulties the problem is an attractive one, and the
abundance of material to be had in any desert city, to-
gether with the great mass of data that has accumulated
in the hands of horticulturists and at the experiment
stations, offers the best of opportunities for extended and
fruitful work.

If, as we have seen, the different deportment in the
desert of plants growing, or having the opportunity to
grow, side by side in well watered ground, is an exceed-
ingly complicated matter, by how much are the difficul-
ties increased when we pass from a habitat of uniform
and highly favorable conditions, to the various and often
extremely trying conditions which prevail in different
neighboring habitats, such as the dry slopes underlaid
by caliche, the salt spots and others.   If the case of a
plant growing in well watered soil may become desperate
because of the scorching winds or the intense insolation
to which its top is exposed, what hope is there for one
that assays to grow where both dry air and dry soil pre-
sent the supreme test of endurance?   As a matter of fact
only relatively few species meet the test successfully,
yet there are some that do, and they present some of the

most instructive data yet derived from the study of desert plants.

But little reflection is needed to arrive at the conclusion that the classical question regarding the relative importance of physical constitution and chemical composition of the substratum to plant growth—though like the poor it promises to be always with us—does not, and can not reach the heart of the problem. For every plant which successfully holds its place in a true desert habitat there is a delicate balancing of the regulation of transpiration, the power of absorption, the capacity of the conducting system, the presence or absence of storage tissues, and, we may well believe, the possession of protoplasmic properties which contribute to its powers of endurance. This being the case, it would seem that in future, investigations of the habitat relations, of desert species especially, must be directed mainly to the plant itself. The advantage of a thorough knowledge of soils is too obvious to call for comment, but it must be remembered that we are as yet only at the threshold of a greater and more promising work, namely, the investigation of the physiological requirements and capabilities of plants that can grow in a true desert habitat as compared with those that can not. In such comparative study lies, as it seems, the hope of real progress. It is impracticable for any investigator, at the present time, to mark out a straight path for others to pursue, and it would very properly be regarded as an impertinence were he to attempt this; yet there are certain obvious suggestions that may be offered.

In the first place, important results have already followed the simplest experiments and observations when these have been conducted with exactness and with a definite end in view. To refer to a specific case,—Professor Thornber, of the University of Arizona, undertook a few years ago to compare the habits of certain desert plants as regards germination. It was found that while the seeds of some species germinated at a given

temperature, others could not be made to do so until they had been subjected to temperatures approaching the freezing point. These latter were seeds of winter annuals, and by this method a fundamental physiological difference between them and the summer annuals was established. Doubtless an indefinite amount of instructive and necessary work remains to be done in this direction, but the key to the situation was found in carrying out the simple experiments described. Again, partly as a relief from severer work, Dr. Cannon undertook, in the midst of his investigations at the Desert Laboratory, to map the distribution in the soil of the roots of some of the plants growing in the vicinity. Hardly was the work well in hand, and the root topography of less than half a dozen species mapped, when it was found that the clue to certain facts of distribution, blindly observed up to that time, had been discovered. I have spoken of this in more detail in another connection.

Obviously it is indispensable that determination of physiological data and of those belonging to the physical environment should proceed step by step together; and nowhere is this more strikingly true than in the investigation of soil relations. To refer to one more case of recent experience,—within the past year Dr. Livingston has determined the percentage of soil moisture present in soils obtained from each of the topographic areas of the Desert Laboratory domain and the adjacent flood plain of the Santa Cruz River. His studies were conducted independently, though naturally not in ignorance of ecological studies which were being carried out at the same time on the same ground. It now appears that a well-nigh perfect correspondence exists between the two sets of facts obtained by independent workers, so perfect, in truth, that a causal relation offers the only satisfactory explanation. The accumulation of physical data, however, has proceeded so far and so satisfactorily that the successful conduct of this line of investigation may be regarded as assured, but for the plant the relations

are more complicated, and their investigation correspondingly more difficult. It seems likely that in the study of ecological relations from the side of the plant we shall employ more and more the methods and conceptions of physics and mathematics, but the fact is too patent to call for argument that neither now nor hereafter can these methods and conceptions be employed exclusively. In fact there has never been greater need than at the present time for exact observation coupled with correct judgment, and these can never be replaced or superseded so long as this department of botanical investigation continues to be cultivated. This will receive additional emphasis in the following division of the present paper.

The relations of desert plants to each other present a chapter, the importance of which has been unduly minimized until the general impression, even among botanists, seems to be that desert plants are to be studied only in relation to their physical environment; they are thought to grow so far apart, in "open" associations, that they are quite uninfluenced by each other's presence. Like other erroneous or incomplete conceptions, this may be true in part, especially where the most extreme desert conditions prevail, as for example in parts of the Colorado or Mojave Deserts, but in the great semi-arid region of the southwest, taken as a whole, it is most misleading. The Desert Laboratory of the Carnegie Institution was located where it stands on account of the great natural advantages which the region and locality offer for the study of desert plants in place, yet I venture the assertion that over at least nine tenths of the area of the laboratory domain the establishment of a plant in the place which it occupies is conditioned quite as certainly by the influence of other plants as by that of the physical environment. It hardly needs more than simple observation to convince one that severe competition is the rule, though naturally its severity is heightened and the result hastened by the prevailing adverse physical conditions.

Beginning with some of the most obvious cases, the winter annuals of southern Arizona present an instance of as unmistakable competition of individuals with individuals and species with species as can be found in the eastern forest region of the United States. As the warmth of spring follows the winter rains the ground is thickly carpeted with *Amsinckia, Pectocarya, Bowlesia,* and various other herbaceous plants, which stand thick together and present to the eye the familiar crowding which is seen in a field of grain too thickly sown. Certain individuals dwindle and finally die, robbed of water, food and light by their stronger competitors. It might be interesting to repeat the experiment in the laboratory and to tabulate the results statistically, but it could hardly add to the conclusiveness of the demonstration. The same is true of the manifest competition of species with species, as seen for example in the occupation of relatively extended areas by some of the perennial grasses which, but for their presence, would certainly be covered, as the adjacent areas are, by a thick growth of other plants. Here the actual advance of the grasses from year to year may be observed, and such observations for the sake of more definite statement are now in progress on the Desert Laboratory domain. Convincing evidence of competition is thrust upon one's attention in passing from the desert to areas beyond its borders, and if the transition is abrupt, as for example on the western edge of the Salton Basin, where the desert abuts almost upon a mountain wall, the case is all the more striking. In this instance a straight course of less than five miles brings one from the actual desert, with its characteristic sparse growth of salt bushes, creosote bush, galleta grass, and the like, to the chaparral of the mountainside. Along the way the desert species fall out one by one, and are replaced by elements of the chaparral. As far as can be judged by their habits elsewhere and from their known range in altitude, there is absolutely no reason for this, except their inability to compete with plants of the cha-

parral, which, however incapable of normal development in the desert, hold their own ground, where the conditions are less strenuous, so tenaciously and completely that the desert species make no headway against them.

This, of course, is an interpretation merely, but with such an accumulation of evidence we are now in a position to proceed with the problem along definite lines with the expectation of definite results. Sowing together seeds of desert and other plants, the transference of individuals to denuded areas beyond their natural limits, and multiplied comparative observations of the deportment of different species on the ''edge of the desert'' are simple and obvious methods of procedure at the outset. Some of this work has already been done, enough to convince those engaged in it that in general the problem of the successful occupation of a desert habitat involves the recognition of actual competition on the part of its would-be occupants, a competition severe enough in some quarters to set up a barrier beyond which, in the midst of otherwise entirely favorable environmental conditions, they can not pass.

In their relations to each other, desert plants frequently exhibit not merely competition but accommodation. This has been clearly shown by recent studies of the root systems of certain cacti and other plants by Dr. W. A. Cannon. To take a striking example—superficial observation of the association of the sahuaro (*Cereus giganteus*) with one of the palo verdes (*Parkinsonia microphylla*) and some other shrubby perennials gives no satisfactory clue to the reason of this relation, and the common explanation that they are plants of similar biological requirements, and therefore grow together, is altogether inadequate and in part misleading. The careful study, however, that has been given to the root systems of these plants brings out the important fact that they grow close together by virtue of simple accommodation, which enables them to utilize to the utmost the scanty rainfall. The roots of the sahuaro are spread

just beneath the surface of the ground, where they take up and promptly pass on to the storage cells of the trunk the water brought to them by every light rain. The roots of the palo verde, on the other hand, extend much more deeply into the ground, and are in a position to utilize the water which soaks down to lower levels after heavier rains. Thus the sahuaro profits by all rains, light and heavy alike, while its constant companion, the palo verde, is free from all competition on its part for the water which penetrates to lower levels. Much the same thing is seen on the flood plain of the Santa Cruz and other rivers, where the mesquite, with its deep roots reaching to the water table, is associated with *Bigelowia* and other plants, the roots of which extend to relatively shallow depths. In short, it appears that just as in a tropical forest the vegetation occupies successive "stories," so here the root systems of various plants habitually reach to different depths, and thus enable at least some species that would otherwise compete with each other to live in close and advantageous association.

From what has been said, it is evident that in the successful occupation of a desert habitat the mutual relations of the associated species play a highly important part. It is not quite easy at this stage of progress to point out the exact steps by which these complicated relations are to be determined and estimated; meantime the homely and effectual method of patiently gathering the data that are obtainable by careful observation is open, and as far as it has been pursued has yielded valuable results.

The broad general problem of the local distribution of desert plants is necessarily approached along the several lines that have been indicated. As we have seen, atmospheric conditions, whether of intense insolation or extreme dryness, that obtain in arid regions are limiting factors which many plants successfully meet, but to which many others succumb. There has been great need of more practical methods of determining and estimating

the influence of atmospheric factors, and it is a matter of congratulation that the methods devised by one of the participants in this discussion, already widely in use in different parts of the United States, promise to meet this need to a degree that could not be hoped for at an earlier period. But it is never to be forgotten that under the same atmospheric conditions, and with equal chances in other respects, the deportment of two plants side by side, their capacity for adjustment let us say, is so different that the essential problem lies first of all in the physiological capabilities of the plant itself.

More strikingly true, if possible, is this seen to be the case when the relation of desert plants to the soil is considered. It is well that so much soil work has been done, that we have soil maps, that determinations of water capacity and other physical as well as chemical characteristics have been ascertained in so many habitats, and that we have a growing literature embodying observations of the relations of plants to underlying rocks, in short that the substratum has been the object of so long and so thorough study; there is no danger that we shall have too much of this, but there may be danger that we may sometimes forget to place the emphasis where it belongs, namely, on the fact that every species and every variety of plant is a law to itself in its relations to rock or soil. It is true enough that the different percentages of alkali salts at different distances from the center of a salt spot stand apparently in causal relation to the growth of different plants in corresponding concentric zones, but it is equally true that this zonal arrangement is also the visible expression of the capacity of these different plants to cope with the conditions there existing, and of this capacity, if it is to be expressed, as some day it must, in physical measurements, how inadequate is our knowledge. How greatly we need to really know the physiological constants, not of one but of many desert plants.

It is in the same line of thought, and with the same purpose, that I have referred to the inadequate concep-

tion according to which the relations of desert plants to
each other have been so persistently overlooked or at
least underestimated. It may now be set down as an
established fact that over a large part of the arid or semi-
arid territory of the southwest, competition on the one
hand and accommodation on the other have much to do
with the association of plant species and the density of
the plant cover. Far more, it would seem, than has
usually been thought, the character of various associa-
tions in this region is determined not simply by the
physical but also by the living environment. More than
ever too, it is plain that the path of progress lies in the
direction of applying to the plant itself, in its natural
surroundings, the experimental methods of the physical
laboratory. Notable and fruitful beginnings have been
made in this direction, but one who has attempted quan-
titative work with the sahuaro or ocotillo in the open
need not be told that it involves difficulties not presented
by seedlings of *Vicia faba* grown in pots, and that prog-
ress will necessarily be slow.

Thus far adjustment and adaptation have not directly
entered into the discussion, although a moment's thought
shows that all the paths along which we have come con-
verge right here. If one variety of geranium flourishes
in the desert air, while another by its side dwindles and
dies, we can only say at present that the latter is not
"adapted," or is apparently incapable of "adjustment"
to the atmospheric conditions in which it has been placed.
We find that plants growing in the wash near the Desert
Laboratory do not, as a rule, succeed in gaining a foot-
hold on the long slope leading to the hill near by; they
are not adapted to the soil conditions there existing; but
the creosote bush, which makes its home on these slopes,
grows—thanks to its capacity of adjustment—even more
luxuriantly in the wash than on its own domain. Simi-
larly, certain plants of the salt spots grow better beyond
than within their limits; they have become adapted to
large percentages of alkali salts, but their capacity of

adjustment is such that they grow just as well or better along an irrigating ditch carrying fresh water. Various other plants in the immediate neighborhood have not become adapted to the conditions prevailing in the salt spots, nor do they appear capable of adjustment to them, and accordingly are not found growing in such places.

We need not multiply citations of these familiar cases. Adaptation and adjustment have long been words to conjure with, out of the desert as well as in it, but we have made so little real scientific progress in the definition and determination of the things for which they stand, that some of our foremost students of ecology seem ready to abandon the effort, while others apologize when they use the terms, as if they were myths and had better be left alone. But nothing is gained, and much may be lost, by this method of procedure. We are face to face with a great body of phenomena of the most striking character, in connection with which these words are fittingly employed. We can not ignore the existence of the facts, and as scientific men we can not let them alone, while they insistently rise at every turn in our pathway and demand investigation. True it is that they bring in their train whatever is fundamental in biological inquiry —heredity, the direct influence of the environment, and differences in the properties of protoplasm in different plants. It is not customary, however, in laboratories worthy of the name, to shun investigations that approach to the deep mysteries of life. There is every reason why students of ecological problems should seek, not shun, this difficult but hopeful line of study. I say hopeful advisedly, for within the past three years there have come under my observation various definite cases of adjustment in plants, some of which have been accurately measured, correlated with external factors, and expressed by curves. Though essentially more difficult, there is no reason, as far as now appears, why the different degrees of adaptation of two species or varieties to a given external factor may not be similarly determined and

graphically represented, as the expression of a definite difference of physiological activity, as shaped by heredity, in relation to that particular factor. Very little, as far as I am aware, has yet been accomplished in this direction, but it is a way that is wide open, and one that should attract those real investigators who, knowing difficulties, do not shrink from them.

We have considered in a way far from exhaustive some of the problems which specially interest the student of desert ecology, but which in their broader relations are not confined within geographical limits. In the efforts now being directed towards their solution the trend, as it appears to the writer, is not so much away from any previous form of thought or method as towards the wise and persistent use of every means that promises results. Progress is certainly being made in the direction of greater exactness; we are learning something of the possibilities of well-directed cooperation; and in these and other ways in which "science returns to the obvious"—to use the apt words of Francis Darwin—is an encouraging promise for the future.

PRESENT PROBLEMS IN PLANT ECOLOGY

V. The Relation of the Climatic Factors to Vegetation

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1. *The Recent Advance in Point of View.*—Perhaps the most interesting and important advance that has been made during the last decade in the study of the relation of plants to environment is in regard to the point of view. It is difficult to say just when the movement began, but it is assuredly true that it has only recently gained recognition. To a certain extent the movement has involved the substitution of the ecological for the floristic method in geographic problems involving climate. It has resulted in a general dissatisfaction with the older descriptive methods and has tended toward a better appreciation of the value of exactness both in the delineation of vegetation and the quantitative analysis of environmental complexes. The movement has further brought to our attention the necessity for investigating vegetation processes by experimental methods comparable to those by which plant processes have long been studied. As I see it, however, these are secondary phenomena attending the substitution of dynamic and genetic views of vegetation for the century-old static conception of plant distribution.

Fourteen years ago it was possible for one of the most prominent students of the North American biota to say:[1]

It appears, therefore, that in its broader aspects the study of the geographic distribution of life in North America is completed. The primary regions and their principal sub-divisions have been mapped, the problems involved in the control of distribution have been solved, and the laws themselves have been formulated.

[1] Yearbook, U. S. Dept. Agric., 1894, p. 214.

Such a claim could have been made only for a static system, since a genetic conception of the problem necessarily involves the indefinite postponement of the approach toward a final solution.

The appearance of the classics of Warming and Schimper served to impress all with the inherent complexity of the problem. We are no longer deeply concerned with the discussion as to whether temperature or moisture is the more important geographic factor. Neither do we hope to erect a stable system of geographic divisions upon either of these bases. When we recall that for North America alone not less than sixty different proposals of geographic zones and regions have been published during the last century, the futility of the point of view which disregards all but one or two climatic factors and emphasizes boundary lines, must be apparent. But we shall be still more impressed with the inadequacy of these proposals if we attempt to relate the actual distribution of plants or plant formations to these "regions."

Recently there has been a rapid increase of local ecological studies in which the successional processes of vegetation have been emphasized. These studies have apprehended to a greater or less extent the dynamics of the habitat and the plant formation. The separation of the local vegetation into stages has assumed the dominance in each, of a distinct complex of environmental factors. The occurrence of distinct boundaries has neither been assumed nor insisted upon.

Local studies, however, can not lead to general conceptions of vegetation unless compared and united into larger units. This brings us to the fact that the larger units generally recognized are transcontinental zones and regions. But zones and regions are static entities. They are developed upon assumptions wholly different from those upon which the local studies have been founded. Usually in zonal classification temperature is recognized as all-important and rainfall an unfortunate disturber of symmetry. Not a few are based upon phenological as-

sumptions long since proved untenable or still awaiting
experimental evidence.   In other words, the succession
of local plant formations which has consciously depended
upon changes in the concomitant action of many soil,
climatic and historical factors, is made to fit into a larger
unit whose fundamental basis is a single or at most two
climatic factors.   It is to be noted further that the prob-
lem most debated in connection with zonal arrangements
is the boundary; that the term ''zone'' implies uniformity
of structure and homogeneity of composition.   But the
most striking fact about the geographic distribution of
individual species is their dominance in some region and
their decline in importance and frequency as we depart
thence in any direction.   Plant formations in their dis-
tribution show the same phenomenon.   Further, it ap-
pears that the optimum areas of scores and hundreds of
species nearly coincide.   In brief, actual plant distribu-
tion, through its lack of uniformity and homogeneity, its
tendency to concentric dispersal, and the coincidence of
the optimum areas of many species, seems to demand
larger units in harmony with the processes, structure,
composition and origin of their components.   Whether
we choose to call them ''centers of dispersal'' is of small
moment, as compared with the recognition of the fact that
zones and their sub-divisions are not natural organiza-
tions of plants or plant formations.   Of course, this
criticism does not refer to the use of the very convenient
expressions of certain spatial and temperature concepts,
viz., torrid, temperate and polar zones.

The unsatisfactory character of zones as a basis for
classification is felt also by students of climatology.
Especially is this true of the classification of the climatic
types prevailing on continents.   The schemes of Hult
(1892–3), Koppen (1900), Supan (1903) and Herbertson
(1905) are especially interesting in this connection.[2]
Further, the provinces pointed out by Supan for North

[2] Ward, R. DeC. ''Classification of Climates,'' *Bull. Amer. Geog. Soc.*,
38: 401–412, 465–477, 1906.

America show a remarkable coincidence with the natural vegetation centers. If future work both on climate and plant distribution should bring these fundamentally different view-points into essential agreement we should have the possibility of a completely dynamic and genetic system of vegetation and climatic units.

2. *Sources of Error in Applying Climatic Data.*—One of the sources of confusion in the use of the climatological data supplied by the Weather Bureau, in connection with vegetation studies, lies in the placement of the instrument shelter. The data derived recently by means of recording instruments placed in various topographic situations, show such great comparative variations, that the applicability of meteorological records made under the conditions represented by some of the weather stations may be called into question. Fortunately descriptions of the climatological stations of the United States are now available[3] and selection of stations which truly represent the conditions of at least one local habitat may be made.

A second source of error in the comparison with vegetation of climatic data as represented on charts is the fact that the means do not always represent actual local conditions, but may have been corrected for altitude above sea level. Such corrections, however, have not been made, except in the case of the barometric pressure maps, in the recent climatological bulletin of the Weather Bureau.

3. *Recording Instruments for the Measurement of the Climatic Factors.*—The increasing number of those who are attempting to secure by means of recording instruments, habitat data regarding temperature, relative humidity, etc., is the most hopeful sign of progress in the solution of the climatic problems of plant distribution. We now have fairly satisfactory recording instruments for temperature, humidity, rainfall and sunshine. The porous cup atmometer recently added to this list places

at our disposal a recording instrument whose importance
can not be overestimated.   Because of its directly appli-
cable data, its slight cost and ease of manipulation, it may
well take precedence in comparative habitat investi-
gations.

The greatest desideratum in the way of habitat study
now seems to be an instrument for the measurement of
light values.   It seems probable that the effects of the
varying light intensities and qualities in the habitat are
generally underestimated at the present time.   The com-
parative studies already made with actinometers and
photometers are suggestive, but the value of the data as
indicative of relative light conditions from the standpoint
of vegetation is open to serious question.   Thus far
photographic papers have been most generally used.
Aside from the high percentage of error attending the
matching with standards of the colors developed, these
papers are almost wholly affected by the most refrangible
rays of the visible spectrum.   Plant functions in general
find their optima among the least refrangible rays.   Ow-
ing to selective absorption, a decrease in the intensities of
one portion of the spectrum does not necessarily imply
a similar decrease throughout.   The objection urged
against photographic paper also holds for the use of other
substances which develop precipitates or gas pressure
under the influence of light.   Unless papers can be de-
vised which have an increased range of sensitiveness and
which can be used in connection with color screens, the
continuance of actinometric measurements in habitats
seems almost a gratuitous pursuit.

Naturally the spectro-photometer has been suggested
for overcoming this difficulty.   By means of photographic
methods, in which a diffraction grating is used for the
dispersion-piece and photographic plates of known sensi-
tivity to the various light rays, more accurate results
might be obtained.   The difficulties of manipulation, how-

ever, seem to preclude the use of this method at the present time.[4]

The method suggested by Zederbaur of using a spectro-photometer in connection with colored prisms and a standard lamp has been hailed by some as a solution of this problem.[5] It also involves several important sources of error, but these may not prove to be insuperable. This method has the great advantage over the actinom-eter in that it takes into account light quality. With certain modifications, some of which are suggested by Zederbaur, this instrument may prove to be a step toward a better means of light measurement.

4. *Some Climatic Problems of Vegetation.*—But even if the time is approaching when it may be possible to obtain both qualitative and quantitative estimates of the climatic factors related to vegetation processes, we should regard this merely as a preliminary to more important investi-gations.

We have as yet almost no observational or experimental data from a modern point of view, on geographic varia-tion as related to climate. The reports concerning the results of the cultivation of certain varieties of agricul-tural and horticultural plants suggest a large field for the application of experimental methods.

A fundamental consideration in experimentation along this line is the use of pedigreed plants. It seems possible that many of the discordant results obtained by physiol-ogists may be traced to physiological races within the species. The use of seeds from the same plant, branch, or fruit is not sufficient caution unless the pollination has been guarded. Where the growth of such large numbers of plants as would be essential to an experiment in geo-graphic variation is necessary, the results could have little value unless the plants used had been analyzed by

[4] Wallace, R. J. ''Studies in Sensitometry,'' *Astrophysical Journal,* 25: 116, 1907.

[5] Zederbaur, C. ''The Light Requirements of Forest Trees and the Methods of Measuring Light.'' English translation. *Forestry Quarterly,* 6: 254, 1908.

scientific plant-breeding methods and been shown to consist of an elementary species or variety.   Too much insistence can not be placed on this point.   The use of homogeneous material is an indispensable prerequisite.

If the experiments are to contribute to the better understanding of the greater vegetation units the experiment stations will need to be critically located.

Probably the most promising field for experimentation at the present time is the investigation of the processes of vegetation.   There are so many vague notions and dogmatic statements regarding the processes of competition, migration, adjustment, etc., in relation to the climatic factors, that the rewards for pioneer work will be ample.   Here again the methods and materials must be carefully considered.   In certain of these problems pedigreed (or better perhaps standardized) plants will give far more definite conclusions than those whose composition is unknown.   In others, the more nearly we approach actual habitat conditions and investigate actual habitat processes, the more useful will be the results.

Experiments thus guarded may lead not only to a better understanding of vegetation, but they will also contribute to the science of evolution.   If the methods used will bear inspection both from the standpoint of the process of heredity and from the processes of vegetation, natural selection and adaptation may be resolved into processes of more definite meaning.

The recognition of the importance of the results of ecological investigations in the practice of agriculture, horticulture and forestry has added much to their intrinsic interest.   Some of the problems are perhaps beyond the reach of the individual worker.   Fortunately there are several institutions in the United States within whose scope these problems lie.   That they have already begun the publication of contributions to this field is the best evidence that both the larger and the smaller problems of the climatic relations of vegetation will be more adequately studied in the near future.

NOTES AND LITERATURE

RECENT EXPERIMENTS ON THE INHERITANCE OF COAT COLORS IN MICE

The domesticated varieties of rodents, rabbits, guinea-pigs, rats and mice, have furnished exceptionally favorable material for analyzing the facts of Mendelian inheritance. The simple formulæ that at first sufficed to explain the results have become more complex as the work has progressed until, at present, the situation has become not a little intricate owing to the different interpretations that the facts have received. This complication is, however, paralleled by progress in the study of plants, fowls, pigeons, sheep, swine, beetles, moths, snails, etc. Despite the elaboration that Mendel's originally simple law has undergone, it is significant how little there is in later discoveries that is believed to be incompatible *in principle* with this law, which may seem to vindicate itself in every direction where new facts come to light. This is nowhere better illustrated than in the latest facts and newest theories relating to inheritance of color in mice.

The earlier work of Allen, Darbishire, Davenport and Cuénot has given the relative order of dominance of the colors. These stand yellow (Y), gray (G), black (B), chocolate (Ch) and white (W). Each color is dominant to all that follow it in the order given and recessive to all that precede. Cuénot's results with white mice—albinos—showed that albinos stand in a class by themselves. White mice may carry *latent*[1] the factor for producing any color, although so long as white mice are mated, they produce only white. Cuénot's suggestion has been widely adopted, namely, that two factors are essential to produce any color; one of these is common to all colors and is called the color producer (C), the other is specific for each special color (Y, G, B or Ch). When C is absent, no color can arise, although the other factor, the determinant, may be present; hence white mice are characterized by the absence of the color producer (C)

[1] The term " latent " has come to have another significance in recent work. In general it now means the presence of one factor only when two are necessary for the development of a character.

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although they carry one or more of the color determiners. In fact no white mice are known in which all determiners are absent, and from the nature of the case none could arise. An example may make this clearer. It is assumed that white mice first arose by the loss of the factor C. Suppose this occurred in a gray mouse, CG. It would then contain only the factor G and no C. For convenience the absence of C is represented by the letter A. It might appear that nothing—no symbol—would better represent this condition, but in practise it is convenient to indicate the absence of C; or in other words, to represent the paired character (negative here) of C. A, therefore, is the allelomorph of C, *i. e.*, C and A form a pair of contrasted characters. An example will again make this evident. A gray mouse CG crossed with an albino mouse AG, produces a colored mouse with the formula, CGAG. In the germ cells of this mouse the contrasted characters are $\frac{C}{A}$ and $\frac{G}{G}$, which give, as possible combinations, CG and AG. If we suppose two such mice, male and female, are paired, the possible unions of their germ cells may be represented thus:

$$
\begin{array}{cc}
\text{A G} & \text{C G} \\
\text{A G} & \text{C G} \\
\hline
\text{AGAG} \quad \text{A G C G} & \\
\text{A G C G} \quad \text{CG} & \\
\hline
\end{array}
$$

1AGAG; 2AGCG; 1CGCG

The first term is a pure albino (extracted recessive); the second, a gray mouse carrying white recessive (a dominant recessive or heterozygote); the third term, a pure gray (extracted dominant). If the A's were omitted in the formulæ the outcome would be the same, but its presence is useful in arranging the contrasted characters in the germ cells; for, C always has A or C as its allelomorph, never G (or any other determiner). Hence the advantage of the symbol A. Failure to arrange the pairs of allelomorphs properly will give results incompatible with the theory.

In another graphic way the utility of representing an absent factor by some symbol can readily be shown. Suppose the characters are carried by certain material bodies in the egg— a purely preformation conception that dominates (or is latent in) all recent Mendelian speculation. If the color determiner is

carried by one body and the color producer by a different one, the pairs of allelomorphs will be $\dfrac{C}{C'}$, $\dfrac{G}{G'}$; every gray mouse carries these two pairs which separate at some time in the germ cells so that each germ cell (egg or sperm) carries one of each, C, G. Now an albino must arise by failure of a germ cell to contain C, the germ cell is simply 0 (zero) G, but since the same body that carried C may still be present (only one of its characters, namely C, being absent) the presence of that body is represented by A.

Let us now work out the case a step further. If this germ cell, AG, combines in fertilization with another germ cell, CG, of another individual, the resulting individual will be CGAG. The allelomorph pairs will be $\dfrac{C}{A}$, $\dfrac{G}{G}$. If such a mouse again pairs with a gray one, only gray mice will result. In time, however, enough mice of the formulæ CGAG will arise so that two such may meet; then and only then will an albino mouse *appear* amongst the gray offspring. Thus the conditions that produce the albino must arise two or more generations before the actual albino mouse is discovered.

This example shows, *on the theory,* how sports of this kind (recessive) that appear in nature are due to conditions that arise in the germ cells of an individual several generations earlier. The only possibility, on the theory, that such recessive sports could appear at once would be when several individuals changed in the same direction at the same time. Then the possibility of two germ cells of the same kind meeting would be realized. Recognizing the rarity of the appearance of sports, one may hesitate to assume that two such forms appear at the same time and pair with each other.

This view is based on the assumption that sports arise by the dropping out of one character in a germ cell. If the absent characters arise in some other way, after the germ cells have met for example, the situation is different, but the assumptions here made are in conformity with present-day development of Mendelian inheritance.

Our case was selected, however, not to illustrate how recessive sports arise and later appear, but to show how absent factors may be represented by bodies that in hybridizing become the partners of bodies containing that factor. Hence the supposed advantage of representing such absent factors by a definite

symbol standing for imaginary bodies; for such bodies, on this
assumption, may carry other characters that remain, even though
one be lost, and these other characters would still be subject to
Mendelian rules and be associated with the absence of a character.

In the earlier work on mice and other forms the different
colors, Y, G, B, Ch, W, are represented as allelomorphic pairs.
Thus Y pairs with G, or G with B, or Y with Ch, etc.   It follows,
that if these color determiners are carried by definite bodies,
these must always be the same kind of body or homologous
bodies; otherwise they would not stand in this relation to each
other.   Thus a gray mouse paired with a chocolate would give a
gray mouse, GCh whose germ cells would give the pair $\frac{G}{Ch}$.   Two
such mice paired would give:

$$
\begin{array}{cc}
G & Ch \\
G & Ch \\
\hline
G\ G & G\ Ch \\
& G\ Ch \qquad Ch\ Ch \\
\hline
1\ G\ G, & 2\ G\ Ch, \quad 1\ Ch\ Ch
\end{array}
$$

Similarly for every other combination.   As a matter of fact
gray by chocolate gives not only gray and chocolate but some
black mice in the second generation.   The formulæ fail to
explain this result.   Bateson, who was one of the first to point
this out, was led therefore to a new formulation of the facts, and
Cuénot to still another.   Their views will be given later.

Another difficulty in connection with the inheritance of yel-
low was soon discovered by Cuénot.   Yellow mice bred to yellow
give not only yellow, but other colors as well.   This would occur,
of course, if the yellows were heterozygous.   Thus YG by YCh
would give yellows (YY, YG, YCh) and grays (CG).   Some of
the yellows should be YY, and two such paired should give only
yellows.   Cuénot was unable to produce such pure yellows.   He
therefore adopted a special explanation (selective fertilization)
for this case.   His view will come up again later.

A third complication arose in the case of dilute colors.   In
certain experiments, that need not be given here in detail,
Cuénot found that the only assumption that would account for
the facts was that two other factors—a strengthening or enforc-
ing character (foncé) F, and a weakening or diluting factor

(dilué) D. The presence of F changes chocolate to black, the presence of D (in the absence of F) changes black to chocolate, and chocolate to dilute chocolate (or silver fawn).

In certain races of colored mice, the eyes are pink (absence of pigment) as in albinos. The presence of the factor that produces this condition has an effect on the coat color, according to Cuénot, hence he introduces a further set of factors that affect the color. By means of these several factors the inheritance in complex cases was explained.

It has been pointed out that in all gray rodents the color gray is due to a banded or barred condition of each hair. Each hair, in fact, contains bands of yellow, black and chocolate, arranged in definite sequence and in definite regions of limited extent. Hence gray is not a color in the sense that yellow or black or chocolate are colors, but is made up of all three. It is their arrangement that is the chief agent in producing gray animals. For this reason Castle has introduced a further factor, a barring or ticking factor instead of a gray factor. Hence gray is no longer allelomorphic to the other colors, but these colors are characterized by the absence of the barring factor and by the presence of one (or more) of the other colors.

Finally the hairs of black mice are known to contain chocolate pigment, so that black is not strictly allelomorphic to chocolate, although crossed with chocolate the Mendelian ratio for black and chocolate appears.

These and other discoveries show that the first representation of the pairs of characters will no longer suffice to account for the conditions that exist, although they give the Mendelian expectation for the cases first studied. We may next proceed to examine in more detail the hypotheses advanced to meet the more complex situation.

Bateson and his co-workers have discovered certain cases of inheritance which have led them to assume that *in crosses* the allelomorph of a given character is the absence of that character. For mice the following symbols are used:

> CGB .... Gray or agouti
> CgB .... Black
> CGg .... Cinnamon agouti
> Cgb .... Chocolate

So long as gray is bred to gray each character has its like for its allelomorph; $\dfrac{C}{C'}$ $\dfrac{G}{G'}$ $\dfrac{B}{B}$. But each germ cell will contain only one C, one G, one B. Similarly for any other color bred to its like.

If gray (CGB) is bred to chocolate (Cgb) the resulting mouse has the composition CGBCgb. The allelomorphs are $\dfrac{C}{C}$, $\dfrac{G}{g}$, $\dfrac{B}{b}$. These hybrids bred together give the results shown in the next table. The possible germ cells of each will be CGB, CGb, CgB, Cgb, which by combination give the results here shown: 12 grays, 3 blacks, 1 chocolate.

CGB CGB gray	CGB CGb gray	CGB CgB gray	CGB Cgb gray
CGb CGB gray	CGb CGb gray	CGb CgB gray	CGb Cgb gray
CgB CGB gray	CgB CGb gray	CgB CgB black	CgB Cgb black
Cgb CGB gray	Cgb CGb gray	Cgb CgB black	Cgb Cgb chocolate

Thus the black mice that appear in this cross in the second generation are due to the absence of G and to the presence of the factor B. The single chocolate amongst the 16 mice is due to the absence of both G and B in the presence of C. Hence, Miss Durham recognizes chocolate (Ch) and color factor (C) as the same. Cuénot accounts for the results as follows. The gray mouse has the strengthening factor F along with C and G. The chocolate mouse has the diluting factor D along with C and Ch. The combination gives FCGDCh. The pairs are $\dfrac{F}{D}$, $\dfrac{C}{C}$, $\dfrac{G}{Ch}$. Omitting C, present in all combinations, we find the possible combinations are FG, FCh, DG, DCh. Two such mice crossed give the kinds of offspring shown in table on page 500.

The results are 9 gray, 3 dilute gray, 3 black, 1 chocolate, and these are the actual numbers realized. The dilute grays are grays without black and are known as cinnamon agoutis. Whenever F occurs with Ch the combination gives black, whenever D occurs alone with Ch (once) the result is chocolate.

FG	FG	FG	FG
FG	FCh	DG	DCh
gray	gray	gray	gray
FCh	FCh	FCh	FCh
FG	FCh	DG	DCh
gray	black	gray	black
DG	DG	DG	DG
FG	FCh	DG	DCh
gray	gray	gray	gray
DCh	DCh	DCh	DCh
FG	FCh	DG	DCh
gray	black	gray	chocolate

Both hypotheses account for the numerical outcome. Some other criterion must decide between them. The criterion is found in the recent work of Miss Florence M. Durham who has pointed out that chocolate can not be dilute black, since a dilute form of black is known, which is quite different from chocolate.[2] Let us examine her results.

Black and chocolate are found either in a dense condition when the mouse is called black or chocolate, or in a dilute state, *i. e.*, with the pigment granules scattered. Dilute black is blue and dilute chocolate is silver fawn in the "fancy." Black dominates blue and chocolate dominates silver fawn on the older terminology. But it is known that black mice often contain chocolate whose presence is obscured by the darker color, black. This relation Bateson calls epistatic. In the same sense black is epistatic to blue; and chocolate is epistatic to silver fawn.

Black crossed with blue gives black only. Such heterozygous blacks inbred give 3 blacks to 1 blue. Similarly chocolate crossed with silver fawn gives chocolate. These inbred give 3 chocolate to 1 silver fawn.

The most interesting result reported by Durham, is seen when black, *i. e.*, blue, is crossed with chocolate. The result is black, because the chocolate supplies the strengthening factor and makes the dilute black dense black which is epistatic to chocolate.[3] In

[2] There may be two quite distinct meanings however attached to "dilute." Cuénot means the black pigment is changed to chocolate pigment. Durham means that the black pigment granules are sparse in the dilute form. See next footnote.

[3] This experiment shows that Durham's interpretation of the dilute color is correct; Cuénot's is incompatible with the experiment, unless the factor for Durham's dilute colors is different from the diluting factor of Cuénot.

the second generation such black mice give approximately

        9 black, 3 blue, 3 chocolate, 1 silver fawn,

which is the Mendelian expectation.

When blues are mated to silver fawns the offspring are all blue. These inbred give three blues to 1 silver fawn.

Miss Durham's hypothesis gives a consistent account of the relation of the dense and dilute colors to each other.

The dilute colors are modified to some extent, as Cuénot first showed, by the condition of the eye color. Most mice with colored coats have black eyes. The black eye is due to black pigment in most cases, but in chocolates and in some yellows the dark eye is due to chocolate pigment, as Castle and Durham have independently found. A silver fawn with pink eyes may be of a different color from a silver fawn with dark eyes. How this modification results is not yet known. In fact, this relation of dilute colors to eye color offers a promising field for further inquiry.

An examination of the hair of dilute mice shows great differences in the amount of pigment in each hair and the color of the animal is modified by the average number of hairs of a given kind. A considerable range of shades is evident. Whether this is only a fluctuating character, or whether pure races of different shades can be made that give Mendelian proportions, if crossed, remains to be worked out. It is not entirely certain, I think, that the pigment granules themselves are not only scattered to varying degrees but may be even lighter or darker. Whether this is due only to size or to another factor is not yet known.

These dilute colors should combine with ticking to produce different shades of gray in addition to cinnamon agouti. Some of the grays that I have met with appear to fall under this head.[4] Whether the diluting factor for black and chocolate will act as a diluter for yellow is not known. Here we meet with a question of great importance in further study of the colors in mice.

In addition to albinos with pink eyes, white animals with black eyes are known to occur in many groups of animals. Such a race of fancy mice exists. Miss Durham reports that these white mice crossed with colored mice with uniform coats produce

[4] Thus cinnamon agouti crossed to silver fawn may produce in the second generation a pinkish agouti with light chocolate in place of dense chocolate.

in the first generation some spotted mice. This result I have also repeatedly obtained. It remains to be discovered what relation exists between the white of such mice and the white of common spotted mice, for in these the spotting disappears in the first generation. It appears that the white mice with black eyes are derived from spotted mice in which the spotting has been carried so far that pigment remains in the eyes alone. If these mice are only extremes of the spotted conditions the results seem to indicate that a recessive character has been changed to a partially dominant one. Perhaps one might say that physiologically it has become stronger. On the other hand, these black-eyed white mice may have arisen not from extremes of ordinary spotted mice but from a different relation between black and white. It is interesting, however, to note that in rats the recessive spotted coat also partially dominates in the first generation.

Cuénot has shown that ordinary spotted mice behave towards mice with uniform coats as a simple recessive, appearing in the second generation as 1 to 3. But I have found in practise that it is almost impossible to give an exact classification of the mice in the F_2 generation. In some individuals there may be only a small white tip to the tail, or only a few hairs may be white. Whether to classify such mice as dominant or recessive is largely arbitrary. White hairs not infrequently appear in mice that seem to be uniform in color. I find them quite abundant in wild black rats (*Mus rattus*). In man they appear in old age, and in horses when the skin is injured, etc. These considerations raise the question whether the problem may not after all be physiological, the result being due to the activity of the cells rather than to the absence of factors in the sense in which that term is ordinarily used in Mendelian hypotheses. If so, the entire result may be one of physiological activity rather than one of presence and absence of factors in a morphological sense.

The inheritance of the yellow color in mice has been a standing puzzle. Cuénot attempted to explain the facts on the assumption that a yellow bearing sperm can not fertilize an egg bearing this color, but can fertilize any other sort of egg. In other words selective fertilization takes place. Hence every yellow individual contains latent another color; it is yellow because yellow " dominates " (?) the other colors. But if selective fertilization can take place in regard to the individual characters

carried by the germ we introduce a conception entirely foreign to the whole Mendelian scheme.   There is no evidence of selective fertilization *in this sense* known elsewhere and it seems a very questionable advantage to introduce the factor into the Mendelian process.   The evidence that Cuénot brought forward in a second paper to show that selective fertilization takes place is open to criticism.   He points out that since half the eggs can not be fertilized by half the sperm, there should be fewer young born when yellow is crossed with yellow than when yellow is crossed with any other color.   His data show in fact a lower birth rate for yellow by yellow than when yellow is fertilized by other colors.   Two objections to this argument may be advanced.   First we must suppose that there are sufficient sperm present to fertilize the few eggs set free at each menstruation. Even if a yellow egg is not fertilized by a yellow sperm it should be fertilized by one of the other sperms.   Second the fertility of the yellow mice is in my experience lower than that of other colors.

In order to avoid the hypothesis of selective fertilization and accepting Cuénot's statement that pure (homozygous) yellow mice do not exist, I suggested tentatively that the yellow-producing factor is not allelomorphic to the other colors, but that the germ cells of yellow mice are represented by the symbols $Y(B)$, $B(Y)$, to take a single example; in other words that yellow and the other color, black in this case, alternately dominate and recede.   In this way the numerical results follow.   I went so far as to suggest, as a theoretical possibility, that a similar mechanism might explain the alternate nature of the germ cells in all Mendelian cases and pointed out how this view could be tested.   I have made one such test with entirely negative results, so that I think this interpretation must be abandoned.

An experiment that I made with yellow mice showed, however, that the yellow bearing germ cells of yellow mice do carry other color factors than yellow, and this result, which is not in harmony with Cuénot's assumption for the behavior of yellow color in the gametes, offers the possibility of a different explanation.   I crossed a yellow mouse with a spotted black mouse of known ancestry—it carried black only.   Some of the offspring were yellow.   Two of these inbred gave yellows, blacks, chocolates and albinos.   Obviously the yellow bearing germ cells

of the grandparent carried the chocolate determiner since this was known to be absent in the black grandparent. Hence the yellow germ cells transmit the determiners for other colors.

Cuénot has objected to this conclusion on the ground that the chocolate grandchild was due to a diluting factor carried by the yellow grandparent. This objection would be valid if chocolate is the dilute form of black, but Miss Durham has shown that the dilute form of black is not chocolate and that chocolate itself has also a dilute form. This relation I have also seen in my experiments. Furthermore had there been a diluting factor in my original yellow, of which there is no evidence, I should have obtained blues and silver fawns in some of the descendants that were inbred for some time but this is not the case.

It is probable therefore that the yellow color is not the allelomorph of the other colors but may be transmitted along with them. Its allelomorph would be in Bateson's sense the absence of yellow. Even this assumption fails however to show why pure yellows do not appear, and we must look still further for an explanation of the behavior of yellow in inheritance.

Castle has made some important suggestions that bear on this question. The gray coat of rabbits is due, according to his analysis to at least five distinct unit characters represented in the formula

$$\begin{array}{c} U \\ | \\ A-C-B-E \\ | \\ I \end{array}$$
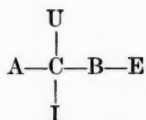
C is the color producer; A is the factor for ticking; B stands for black; U for uniform (*i. e.*, not spotted) distribution of color; I is the intensifier or strengthener; and E a factor that governs the extension of black over the body. For a black rabbit the same formula holds with A left out. For a yellow rabbit E is replaced by R, a factor that stands for the absence of black. A sooty yellow rabbit is like the last with A absent.

It will be noticed that there is no factor in these formulæ for yellow, because yellow is assumed to be present in all these rabbits, but since it has never been *lost* its claim to be looked upon as a unit character is not established. Castle believes that yellow is always present if C is present. Yellow rabbits therefore differ from gray, as stated above in the absence of E (not

of B, black) by which is meant that black is prevented from developing except in the eyes and the skin of the extremities. How far further analysis will justify these conclusions is uncertain, but the interest of the hypothesis lies in the character of the attempted analysis, for the composition of races of different colors is no longer explained as the result of a single color determiner but as the outcome of a considerable number of such determiners. The more recent speculations in Mendelian inheritance show a strong tendency to follow this direction. It might be said that color depends on the absence of certain determiners rather than on the presence of a special one.

It does not appear that Castle's scheme for rabbits will apply to mice unless amended, for the relation of yellow to the other colors appears to be different, and there is no evidence to show that it is present in black or in chocolate.[5]

The most recent attempt to account for the heredity of yellow in mice is that of Hagerdoorn. He points out that there are several kinds of yellow mice, a conclusion familiar to every one that has bred the animals for certain individuals give only certain other colors than yellow in the offspring. I have examples of this in my own experiments. Moreover, one can determine what those other colors may be by crossing yellows with other colors and breeding together the yellow offspring. Hagerdoorn also assumes that, in some yellows at least, an inhibiting factor must be present. This point may seem not improbable[6] from the fact that two yellows may produce in addition to yellows, grays and blacks or chocolates. Since the parents carried the factors for these colors and since they did not appear their absence may be attributed to suppression. So far little exception can be taken to the view since it is in harmony with certain facts. But it is further assumed that the barring factor that determines the distribution of the pigments on the individual hairs is '' composed of two factors, one of which is the modifying factor present in the 'dominant' strain of yellow rodents. Its action, we see, is a partial inhibiting of the two darker pigments whenever these are present with it in one zygote.[7] I therefore propose the name of 'inhibiting factor' for it.'' The other

[5] The grounds for this statement are given later in the case of mice.

[6] Unless yellow is formed by combination.

[7] As shown by the absence of black or chocolate in the yellow band of the hair.—T. H. M.

component of the barring factor is called the "marking factor."
If the marking factor is present and not the barring, the mouse
would be black.   A black mouse therefore contains a yellow
band but this can not be seen because the black and chocolate
pigments obscure it.   If this is correct one would expect to
extract from a black mouse the yellow pigment by a solvent for
yellow.   I shall give below the evidence that negatives this
conclusion.

Hagerdoorn also thinks that yellow may be due in some
cases to the absence of all pigments but yellow.   In such a case
either the marking or the inhibiting factor may also be present
without its presence being noticeable.   The following six classes
of yellow mice are recognized:

(a) Present black, chocolate and yellow plus inhibiting factor.
(b) Present chocolate and yellow plus inhibiting factor.
(c) Present yellow plus inhibiting factor plus marking.
(d) Present yellow plus inhibiting factor.
(e) Present yellow plus marking factor.
(f) Present yellow.

Hagerdoorn states that he has "proof" of the existence of
five of these six groups.   Group (c) alone has not yet been
recognized.   Moreover he obtained homozygous individuals of
each of these groups. Homozygous individuals of the same group
bred to each other produce pure yellow strains, that is, strains
that never produce any other color than yellow.   The reason
that Cuénot and others never obtained pure yellow is due to the
fact that they crossed yellows of different strains and under
such circumstances mice of other colors will appear.   In passing,
however, it should be noted that in Hagerdoorn's classification
of yellows if individuals of strains (a), (b), (d) and (f) were
crossed only yellows should appear in the first and in all subse-
quent generations.   Thus the chance of getting pure yellows
is as four to two, and it does not seem probable with so much
in favor of hitting upon these combinations that such strains
would not have been obtained by Cuénot or Durham, who have
studied the problem extensively.

Hagerdoorn's evidence in favor of his classification of yellow
is obtained by crossing yellows, not with each other, but with
mice of other colors or with albinos of known (?) composition.
The pairings are too complicated to discuss here in detail and in
the absence of numerical data, to show how often the results

cited occurred it would not be profitable to attempt to go further
into the matter.   One example alone of extreme importance may
be cited.   One yellow male mated to chocolate gave only choco-
late young; the same male mated to black gave only black young.
If the number of young is large enough to establish the case con-
clusively it is a distinct advance in our study of yellow mice.
Hagerdoorn assumes that this yellow male contains yellow alone
and that neither the barring nor the inhibiting factor is present.
Hence the cross with black gives only black because the black
obscures the yellow in the hair.   Similarly for chocolate.   If
this is the correct interpretation as much yellow could be ex-
tracted from these hybrids as from a yellow mouse but this test
was not made.   The only other possible conclusion would be
that not enough young were obtained to show that yellows were
not produced by this pairing.   We must await the publication
of the numerical data.   It should be added that the yellow male
was tested by crossing with an albino strain possessing the bar-
ring factor and only yellow young appeared.   This shows the
absence of black or chocolate in the yellow, for were they present
some gray mice should have appeared according to the hypoth-
esis.   Whatever discoveries the future has in store for us these
experiments are of great interest, especially in so far as they
point out a better method for studying yellows than any so far
reported.   The assumption that yellow pigment is present in
black and chocolate can be readily tested.   I have made such
a test and find that black hairs put into caustic potash give no
evidence of yellow to the extent that yellow exists in yellow hair
as shown by the same solvent.[8]   The fact that caustic potash
also extracts chocolate to some extent complicates the result.

The hypothesis seems also to call for the presence of yellow
pigment throughout the gray hair and not only in the yellow
band.   It is more difficult to test this view and observation
would be of no avail since the yellow might be obscured by the
presence of black or chocolate.   It is a point of no small im-
portance to remember that if an inhibiting factor combined with
a marking factor gives the barred or ticked hair of gray mice
these factors act at only a particular period in the formation
of the hair by suppressing the development of black and choco-
late, for the tip and the base of such a hair are dark.   If mark-

[8] Whether some blacks exist without yellow is a further question not
touched by this test.

ing here and elsewhere in animals is due to factors of the sort postulated they are controlled (?) by a periodic function of the hair bud. We meet here with the same problem the embryologist encounters in proportionate development or interrelation of the parts. Whether this is a dynamic *function* (epigenetic) or can be referred to a system of *factors* in the germ is a difficult problem and for the future to decide.

Before leaving this question of yellow mice a few well known facts may be stated. Yellows exist from a deep orange to a pale lemon yellow. All intermediate gradations may be found. Whether these are in reality a graduated series or a series of overlapping conditions we do not yet know. The presence of other pigments combined with yellow is also familiar to every student of these mice. If yellow is due to an inhibiting factor that factor must at times very imperfectly do its work of inhibiting. I have a race of sports of the house mouse with white bellies, gray backs and yellow sides. The hairs on the sides may be pure yellow, which should be due to the action of the inhibiting factor in this particular region only, since on the rest of the upper surface the hairs are ticked. Even in gray mice single hairs may be yellow.

In some yellow mice the belly is pure white. This must be due to a further factor that in this region inhibits the yellow, the yellow itself being the result of another inhibiting factor. In other words an inhibitor of yellow must also be postulated. It might be assumed of course that the white belly is due to the absence of yellow in the region, but since the mouse can produce yellow its absence in the belly must also be accounted for by some special assumption. Again we meet with the localization factor—a problem that Mendelian studies have scarcely yet approached except by the purest symbolic representations.

The fact that many rodents change the color of their hair according to age indicates that the physiological condition of the animal is an important factor in determining its color. If the mechanism of Mendelian inheritance involves only the shuffling of morphological determinants, as implied in many current conceptions of the mechanism of inheritance, the changes that take place in the same individual are difficult to understand unless it be admitted that temporal and local conditions affect the development of the determiners. Such an admission is practically equivalent to referring the development of a color,

for example, to the *extent* to which physiological (chemical) processes are carried out in an individual or part of an individual. Inheritance from this point of view would be a physiological process depending on an inherited degree of activity of the protoplasm (subject to local modifications) rather than the result of sorting out of morphological unities.

Since the preceding review and criticism was written an important paper by Oscar Riddle has appeared in which he takes the same position that I have done elsewhere[9] in regard to the process of Mendelian inheritance. He bases his criticisms on some facts concerning the changes that certain melanin colors undergo as the result of the stage of oxidation to which they are carried. If what happens outside the body furnishes any hint in regard to what takes place in the formation of color in animals and plants these facts rehearsed by Riddle are of great importance in relation to the inheritance of color-production. He writes:

Here is then a *possible* picture of the basis of Mendelian segregation and proportion, but without recourse to hypothetical "particles" or to immutable and immortal factors. An apparently very specific end-result of an oxidation would be traceable in the germ only in the strength or pitch of a general vital process, and not at all in mnemons or representative particles packed with unthinkable precision, order and potentiality into (presumably) the chromosomes. . . The nature of present Mendelian interpretation and description inextricably commits to the "doctrine of particles" in the germ and elsewhere. It demands a "morphological basis" in the germ for the minutest phase (factor) of a definitive character. It is essentially a morphological conception with but a trace of functional feature. Although heredity is quite surely a functional process of major complexity, it may be recalled that the primary and fundamental Mendelian conception of this process utilizes not a single finding of the science of biochemistry, . . . With an eye seeing only *particles,* and a speech only symbolizing them, there is no such thing as the study of *process* possible. . . It has been possible, I think, to show by means of what we know of the genesis of these color characters that the Mendelian description—of color inheritance at least—has strayed very wide of the facts; it has put factors in the germ cells that it is now quite certainly our privilege

[9] See Chapter XXVII in my "Experimental Zoology," 1907, where the same problem is discussed in relation to Sex Inheritance; and in my paper "What are 'Factors' in Mendelian Explanations," read January 1909, before the American Breeders Association, Vol. V, 1909.

to remove; it has declared discontinuity where there is now proved continuity; it has postulated preformation where there is now evident epigenesis.

T. H. Morgan.

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SOME EXPERIMENTS IN BREEDING SLUGS

Certain large naked mollusca or slugs, common in Europe, are noted for their numerous and striking color-variations, some of which seem to be correlated with climatic conditions.   Little has been known concerning the inheritance of these color-forms, but Mr. Walter E. Collinge has recently made some experiments in breeding two of the species, *Arion ater* (or *empiricorum*) and *A. subfuscus*. The results of this work are given in the *Journal of Conchology*, the short paper containing them being Mr. Collinge's address as president of the Conchological Society, delivered October 17, 1908. As the publication is available to few in this country, and the facts cited are very interesting, it seems worth while to abstract part of them.

Arion ater is a very large and handsome slug, of which the following color-varieties were used or appeared in the experiments:

(1) *ater,* pure black. I was not quite clear about the meaning

of the expression "typical," as used by Mr. Collinge, but in reply to my question, he writes that in every case it was "the pure black form, not *nigrescens* or *plumbea*."

(2) *castanea*, a brown variety.

(3) *rufa*, a red variety. The reddest forms occur on the continent of Europe. The above three have the body unicolorous, though the foot fringe may vary.

(4) *albolateralis*, with the back black and the sides white, the two colors sharply separated. A very handsome variety, of restricted range, especially common in Wales. Mr. Collinge writes me that the specimens he used were found in the vicinity of Birmingham.

(5) *scharffi*, like *albolateralis*, but the sides yellow instead of white.

In the first experiment, *castanea* was paired with *ater*, and the former laid 39 eggs, of which 24 were hatched and raised to maturity. These proved to be: 12 *ater* (with slight variations in foot fringe), 10 *rufa*, 2 *castanea*. From this lot, *rufa* was paired with *castanea*, and gave 14 in the next generation, of which four were *ater*, eight *rufa* and two *castanea*.

From the pairing of two of the eight *rufa*, fifteen slugs were raised, eight being *rufa*, two *ater*, and five subvarieties of *castanea*. (Mr. Collinge does not explicitly state eight *rufa*, but in a letter he confirms this interpretation of his account.) From the pairing of two *rufa* of the last generation sixteen adults were raised, twelve being *ater*, two subvarieties of *rufa*, and two subvarieties of *castanea*. Thus the experiment was carried to F_4, with results which are thoroughly Mendelian so far as the segregation of characters goes, but difficult to explain in regard to the appearance and proportions of the different kinds. It will be noted that *rufa* was twice chosen for breeding, to the exclusion of the other varieties, and the second time gave many more black slugs than the first. None of the bicolored forms appeared.

In a second experiment two *albolateralis* were paired, giving a progeny of 22 slugs, 20 being *ater* and 2 *scharffi*. This is so extraordinary that I asked Mr. Collinge particularly about it, and he confirms the result as stated. One would expect *albolateralis* to be homozygous, but the experiment shows that it is either heterozygous (in which case the proportions are hard to explain) or the results are incapable of explanation by any

ordinary hypothesis. I can not help suspecting that the parent slug had really paired earlier with a specimen of *ater*, the progeny in consequence not actually having the origin stated. In that case, supposing *ater* to be dominant, the results would not be so anomalous. It is not so easy to explain the results of the first experiment by the hypothesis of previous pairing, as in that, except for the original pair, the slugs were under observation from their birth.

Seeking a possible explanation of the *albolateralis* case, I consulted Dr. C. B. Davenport, who practically concurs with my view, writing: "The result of Collinge's mating is inexplicable to me except upon one or the other of two hypothesis; either that the parents were heterozygous or else, as you suggest, the supposed parents were not the actual ones, and one had previously paired with a black slug. Of course if *albolateralis* is a heterozygote, then striping is dominant as is usually the case and uniformity recessive. Uniform black would then be active in one quarter of the offspring, but the great proportion of pure black speaks against this hypothesis" (litt., March 22, 1909).

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